Spatial patterns in the diet of the Japanese macaque M acaca fuscata and their environmental determinants

Tsuji, Yamato; Ito, Takehiko Y.; Wada, Kazuo; Watanabe, Kunio

REVIEW

Spatial patterns in the diet of the Japanese macaque *Macaca fuscata* and their environmental determinants

Yamato TSUJI* *Primate Research Institute, Kyoto University, 41-2, Kanrin, Inuyama, 484-8506 Japan. E-mail: ytsuji1002@gmail.com*

Takehiko Y. ITO *Arid Land Research Centre, Tottori University, 680-0001 Japan. E-mail: ito@alrc.tottori-u.ac.jp*

Kazuo WADA *Primate Research Institute, Kyoto University, 41-2, Kanrin, Inuyama, 484-8506 Japan. E-mail: wadakaz@mc.ccnw.ne.jp*

Kunio WATANABE *Primate Research Institute, Kyoto University, 41-2, Kanrin, Inuyama, 484-8506 Japan. E-mail: kuniowatanabe923@gmail.com*

*Correspondence author

Running head: Spatial patterns in the diet of Japanese macaques

Submitted: 1 December 2014

Returned for revision: 27 January 2015

Revision accepted: 4 June 2015

ABSTRACT

1. We aimed to ascertain the environmental determinants of the diets of Japanese macaques *Macaca fuscata* in relation to geographical variables (latitude and elevation) and environmental variables (annual rainfall, mean temperature, snow

characteristics, and normalized difference vegetation index [NDVI], a proxy for primary productivity).

2. We collected dietary data from the entire range of Japanese macaques (29 study sites), and extracted each dietary component to determine spatial patterns over the species' range and between forest types. We then conducted model selection to identify the environmental determinants of staple diets and dietary diversity.
3. Japanese macaques' diets were mainly composed of (1) foliage, (2) fruits and seeds, and (3) bark and leaf buds, throughout the entire range. Percentages of bark and buds were greater in deciduous forests than in evergreen forests; significant differences in the proportions of the other two major components and in dietary diversity were not observed in different forest types.
4. Macaques inhabiting forests with higher NDVI and with less snow fed more on fruits and seeds, and a high dietary diversity was observed. In snowy forests, macaques inhabiting higher elevation fed more on foliage, while those inhabiting lower elevations fed mainly on bark and buds.
5. When studying spatial patterns in the feeding behaviour of mammals, both environmental and geographical variables should be treated equally, since the effect of environmental variables may be independent of the effect of geographical variables. In addition, more emphasis should be placed on snow characteristics, because snow cover leads to decreased availability of terrestrial food items and to increased energy costs (for locomotion and body temperature regulation), which can affect feeding behaviour and dietary diversity.

Keywords: climatic condition, macaque diet, primary productivity, snow cover, spatial

variation

INTRODUCTION

Diet composition is one of the most important aspects of mammalian ecology. Diet influences spatial distributions, social and foraging behaviour, and the body size of animals, and ultimately affects population parameters (Sugiyama & Ohsawa 1982, Iriante et al. 1990, Gende & Quinn 2004, Zalewski & Bartoszewicz 2012). Feeding behaviour, therefore, can be a target of natural selection (Schoener 1971, Stephens & Krebs 1986). Diet studies at local scales, particularly those based on long-term research, have contributed to our understanding of diet-mediated traits, such as home range utilization, inter-group and intra-group competition, and mortality and birth rates (Hill & Agetsuma 1995, O'Donoghue et al. 1998, Tsuji & Takatsuki 2012). However, a complete view of a species' feeding ecology also requires the identification of factors that affect feeding behaviour throughout the species' entire range, because the distribution and abundance of the main food sources often exhibit biogeographical variation (Bojarska & Selva 2012, Díaz-Ruiz et al. 2013). Without studies on spatial variation in diet and associated environmental determinants, we cannot understand fully the ecological adaptations of mammal species with wide geographical ranges.

Many researchers have investigated geographical variation in mammalian diet composition and/or dietary diversity over the last few decades (*Genetta genetta*, Virgós et al. 1999; *Papio* spp., Hill & Dunbar 2002; *Lutra lutra*, Clavero et al. 2003, Remonti et al. 2009; hylobatids, Elder 2004; *Meles meles*, Virgós et al. 2004; *Felis silvestris*, Lozano et al. 2006; *Martes* spp., Zalewski 2004, Zhou et al. 2011; and *Vulpes vulpes*, Díaz-Ruiz et al. 2013). Several researchers have demonstrated significant regional variation in diet composition and/or diversity in relation to changes in latitude and elevation, and between forest types (Zalewski 2004, Lozano et al. 2006, Remonti et al.

2009, Díaz-Ruiz et al. 2013), and have interpreted these relationships as originating in global patterns of availability and diversity of primary food items, such as fruits (Elder 2004, Ting et al. 2008, Moles et al. 2009) and animal prey (Owen 1990, Villafuerte et al. 1998). However, several investigators have failed to find any spatial patterns in diets (Roper & Mickevicius 1995, Virgós et al. 1999). Research has suggested that the proximate mechanism underlying the relationship between geographical variables and feeding is mediated by the effects of climatic conditions, such as temperature and rainfall, on food availability. Hylobatids, for example, in habitats with abundant rainfall, feed more on fruits and less on foliage (Elder 2004). Baboons (*Papio* spp.) spend less time feeding and more time moving in habitats with higher temperatures, and they feed less on fruits in mountainous forests (Hill & Dunbar 2002). However, few researchers have investigated the environmental determinants of spatial patterns in diet composition (Hill & Dunbar 2002, Bojarska & Selva 2012), and whether dietary plasticity is related to the environment is still unclear.

The Japanese macaque *Macaca fuscata* is a primate species that is widely distributed within the Japanese archipelago (Nakagawa et al. 2010). Environmental conditions vary markedly within the geographical range of this species, and Japanese macaques occupy a variety of habitats, from warm temperate to cool temperate regions in latitude, and from the seashore to alpine forests in elevation (Nakagawa et al. 2010). Since food availability and climatic conditions vary not only temporally but also regionally, we hypothesize that the foraging strategies of macaques should vary throughout their range in response to their habitat. For example, the time spent feeding by macaques in northern Japan, in a habitat where food availability is lower, was 1.7 times the time spend feeding in southern Japan (Agetsuma & Nakagawa 1998).

Previous review works of Japanese macaque diets have found spatial trends in their food composition in relation to folivory and frugivory. Uehara (1977) revealed a relationship between forest flora and the diet compositions of 11 different populations, and Tsuji et al. (2013) found that Asian macaques including *Macaca fuscata* that live at high latitudes feed mainly on foliage and less on fruits and seeds, or animal matter, which can be partly explained by differences in annual rainfall and temperature. However, as with other mammals, the environmental determinants that explain the spatial patterns in Japanese macaque diet composition and diversity throughout its geographical range have not been elucidated. This species is the northernmost extant non-human primate, and severe environmental conditions may affect its diet. Wada (1964), Suzuki (1965), and Majolo et al. (2013) highlighted the importance of snow characteristics on the activity and feeding behaviour of macaques inhabiting high latitudes, particularly during the winter. Dietary diversity of Japanese macaques in northern latitudes and at high elevations may be low, since the potential abundance of food in such environments is low (Rosenzweig 1995, Zhou et al. 2011). For example, the dietary diversity of *Lutra lutra* (Eurasian otter) and *Felis silvestris* (wildcat) is lower in northern habitats than in the Mediterranean region (Clavero et al. 2003, Lozano et al. 2006). Similar spatial patterns in diet may also be found in macaques.

In this study, we conducted a comprehensive review of spatial patterns in dietary habits of the Japanese macaque. Specifically, we (1) test whether environmental variables explain spatial patterns in diet composition and diversity, as geographical variables and forest types do, and (2) identify the environmental determinants of the spatial patterns observed in macaque diets.

METHODS

Literature compilation and standardization of dietary data

We conducted a web-based survey of studies in which the diet composition of Japanese macaques was quantified, by using two search engines: ISI Web of Science (http://apps.webofknowledge.com/) and Google Scholar (http://scholar.google.co.jp/). We searched for the key words “Japanese macaque”, “Japanese monkey”, and “*Macaca fuscata*”, in combination with ‘‘diet”, ‘‘feeding”, “food”, and ‘‘foraging’’ (in English and Japanese). We also sought information on the topic from informal discussions with experts on Japanese macaques, and summarized available dietary items in each study site (shown in Tsuji et al. 2011, 2012). In order to standardize our data set, we excluded studies lasting less than one year, and those that contained no information on food categories. Following these criteria, we had information from 29 sites that covered the entire range (30.34–41.15º N in latitude and 60–2340 m in elevation) of the Japanese macaque (Fig. 1). Among them, 13 sites were in deciduous forests and 16 sites in evergreen forests.

We classified food items into seven categories: (1) foliage (including young and mature leaves, shoots of woody plants, and herbaceous plants), (2) flowers (including flower buds), (3) fruits and seeds (including berries and nuts), (4) bark and leaf buds (buds hereafter), (5) fungi, (6) animal matter, and (7) others (including roots, sap, bulbs, honey, seaweeds, and unidentified items). We did not consider provisioned food and agricultural products because these items are not of natural origin. To assess the diet compositions of Japanese macaques, we calculated the relative percentage for each food category (that is, %category $i = n_i / \sum n \times 100$, n = number of food items in a category). We calculated food diversity using the Shannon–Wiener index (H'), obtained by using

the following formula (Begon et al. 2006):

$$H' = -\sum p_i \cdot \log p_i ,$$

where p_i represents the proportion of food category i.

Variable selection

We extracted information on latitude (with 0.1º resolution) and mean elevation (with 10 m resolution) from the source study or from Google Earth (http://earth.google.com) if geographical information was not provided in the study. We defined latitude and elevation as 'geographical variables'.

We obtained data on annual mean temperature (with 0.1ºC resolution), mean annual rainfall (in mm), mean annual length of the period with snow cover (mean number of months with snow cover), and the mean snow depth (in cm) from November to March, which is winter in most parts of the Japanese archipelago (Tsuji 2010). Means of these values for the years 1980–2012, as measured from the nearest weather stations to each study site, were taken from the website of the Japan Meteorological Agency (http://www.data.jma.go.jp/). We used the normalized difference vegetation index (NDVI) as an index of primary productivity. NDVI has strong statistical associations with forest biomass and productivity (Pettorelli et al. 2005, 2011), and has been used to estimate habitat quality (Ito et al. 2005, 2006; reviewed by Pettorelli et al. 2005, 2011). NDVI ranges between -1 and +1; positive values indicate the existence of plants and are related to plant biomass, whereas NDVI values less than 0 are generally indicative of non-vegetated surfaces such as barren land, rock, water, or ice (Pettorelli et al. 2005, 2011). We downloaded 16-day composite and 250-m resolution NDVI data for each study site from the National Aeronautics and Space Administration (NASA), Goddard

Space Flight Center (http://modis-land.gsfc.nasa.gov/vi.html). For each study site, we calculated mean values of the NDVI within a circle with a radius of 2.5 km (ca. 19.6 km^2), which represented a Japanese macaque's mean home range size (Takasaki 1981, Hanya et al. 2006), and calculated the mean of 16 NDVIs from 2002, 2007, and 2012 in spring (7–22 April), summer (26 June to 11 July), autumn (30 September to 15 October), and winter (1–16 January). We extracted the mean NDVIs using the geographical information system software ArcGIS, version 10.1 (ESRI, California, USA).

We defined mean temperature, rainfall, snow depth, snow duration, and NDVI as 'environmental variables'.

Statistical analysis

We compared diet composition and geographical and environmental variables between two forest types (deciduous forests and evergreen forests, see Fig. 1) using the Mann–Whitney *U*-test.

In order to identify the environmental determinants of spatial patterns in dietary traits, we treated the percentages of each food category as response variables, and the 2 geographical variables and 5 environmental variables as explanatory variables, and conducted a series of generalized linear model analyses to select the best-fit models (based on Akaike's information criterion; Akaike 1973). We treated any models with a difference in Akaike's information criterion of less than two as identical (Burnham & Anderson 2002). Before performing model selections, we computed the variance inflation factors for the 7 explanatory variables, in order to check for the effects of multicollinearity (Kutner et al. 2004), but none of the variables was omitted since all

variance inflation factors were less than 10. For the generalized linear models, we assumed that the error structure of the response variables followed a Gaussian distribution, since none of the response variables' distributions were significantly different from normal (Shapiro test, $P > 0.05$). We used R v.2.15.2 (Anonymous 2012) and the "MASS" package for conducting the statistical analyses.

RESULTS

Differences in geographical and environmental variables and diets between forest types

With the exception of annual rainfall, the geographical and environmental variables differed significantly between forest types (latitude: $U = 208.0$, $P < 0.001$; elevation: $U = 161.5$, $P = 0.012$; annual rainfall: $U = 79.0$, $P = 0.282$; mean temperature: $U = 5.0$, $P < 0.001$; snow depth: $U = 205.0$, $P < 0.001$; snow duration: $U = 208.0$, $P < 0.001$; NDVI: $U = 49.0$, $P = 0.012$; Table 1). Deciduous forests tend to be located in mountainous northern regions, with lower temperatures, more snow, and longer winters, and with lower primary productivity than evergreen forests (Table 1).

The diet of the Japanese macaque over its entire range is mainly composed of foliage (26%), fruits and seeds (24%), and bark and buds (25%); flowers (6%), fungi (2%), animal matter (4%) and other items (13%) constitute a much smaller percentage of the diet (Table 1). Among the 7 dietary categories, there were significant differences in the percentage of bark and buds ($U = 200.0$, $P < 0.001$), which was higher in deciduous forests, and in the percentage of other items ($U = 51.5$, $P = 0.023$), which was higher in evergreen forests (Table 1). There were no significant differences in any other dietary categories (percentage of foliage: $U = 77.0$, $P = 0.245$, percentage of flowers: U

= 63.5, *P* = 0.079, percentage of fruits and seeds: *U* = 76.5, *P* = 0.236, percentage of fungi: *U* = 143.0, *P* = 0.090, percentage of animal matter: *U* = 102.5, *P* = 0.905), or in dietary diversity (*H'; U* = 90.5, *P* = 0.568) between forest types (Table 1).

Dietary spatial patterns and environmental determinants

Since general differences in diet between forest types were not detected, more refined analyses were considered necessary, so we attempted to ascertain environmental determinants for the three main food categories (foliage, fruits and seeds, and bark and buds) and for dietary diversity (*H'*). The main determinants of %foliage were elevation (positive effect) and snow depth (negative effect); macaques in forests with higher elevation and/or with less snow fed less on foliage (Fig. 2a, b, Table 2). The NDVI (negative effect) was another determinant of %foliage, though its effect was less.

The main determinant of %fruits and seeds was the NDVI (positive effect); macaques in forests with higher primary productivity fed more on fruits and seeds (Fig. 2c). Snow duration (negative effect) and mean temperature (negative effect) were also determinants of %fruits and seeds, but their effects were less than those of NDVI.

The main determinants of %bark and buds were snow depth and snow duration (both positive effects); macaques in forests with deep snow and long snow duration fed more on bark and buds (Fig. 2d, 2e, Table 2). Mean elevation (negative effect) and latitude (positive effect) were also determinants of %bark and buds, though their effects were smaller.

Finally, the primary determinant of dietary diversity in macaques was snow depth (negative effect); macaques in forests with deep snow had less diverse diets (Fig. 3, Table 2). Mean temperature (positive effect) was another determinant of dietary

diversity, but its effect was relatively less.

DISCUSSION

The lack of relationships between forest types and diet composition (with the exception of bark and buds), and between latitude and main diet composition, differs from results obtained from baboons, which feed less on leaves as latitude increases (Hill & Dunbar 2002), and from Eurasian generalist carnivores, which decrease their consumption of fruit and shift to carnivorous diets with increasing latitude (Virogós et al. 1999, Lozano et al. 2006, Zhou et al. 2011, Diaz-Ruiz et al. 2013). The results of the present study are also in contrast with the findings, in a global-scale review of geographical variation in feeding within the genus *Macaca* (Tsuji et al. 2013), that a negative relationship exists between %fruits/seeds and a positive relationship between %foliage and latitude. The discrepancy between the present study and that of Tsuji et al. (2013) suggests that fine-scale habitat characteristics affect feeding more than geographical variation, and/or that macaques need fruit and seeds or foliage, regardless of their habitat.

The main environmental determinant of %fruits and seeds was NDVI. An association between primary productivity and fruit and seed feeding has also been found in other primates (Hill & Dunbar 2002, Elder 2004), and our study highlights the significance of fine-scale environmental variables affecting diet composition in primates. The number of plant species bearing edible fruit, total fruit productivity, and fruiting duration is higher in forests in lower latitudes and lower elevation; that is, habitats with high primary productivity (Hanya et al. 2005, Ting et al. 2008, Moles et al. 2009). In general, Japanese macaques prefer fruits and seeds to foliage, bark, and buds, because the energy content and ingestion rate of fruits are much higher (Nakagawa

1997, Nakayama et al. 1999). Greater foraging success is an important factor in mammalian reproduction and survival (Fujita et al. 2004, Tsuji & Takatsuki 2012). From this perspective, our finding that the degree of fruit consumption is related primarily to NDVI, a proxy of the primary productivity, is understandable.

The main determinants of %foliage and %bark/buds were snow depth and snow duration. Snow duration was also a determinant of %fruits and seeds: macaques in mountainous habitats with deep snow and/or longer snow duration fed mostly on bark and buds, and less on foliage and fruits. Therefore, spatial patterns in the macaques' bark, bud, and foliage feeding were explained by climatic conditions rather than by patterns in primary productivity. Why did snow only affect the degree of bark and bud (and foliage) feeding? Probably because of the covering effect of snow (Wada 1964, Suzuki 1965): in snowy areas (mainly in northern or mountainous forests), snow sometimes exceeds 2 m in depth (Tsuji 2010) and conceals food items beneath, such as herbaceous plants, fallen fruit, and shrubs. As a result, macaques cannot use these items as food, regardless of their abundance, and they inevitably feed on the only items remaining in the high-tree layer—bark and buds. Another possibility is that snow prevents macaques from moving (Majolo et al. 2013); it is known that macaques in snowy areas have a tendency to perform a low-cost, low-benefit strategy in response to habitat deterioration, including snow coverage (Agetsuma 1995, Enari & Sakamaki 2013, Majolo et al. 2013). In such cases, they shift from foods that are nutritious and result in a high feeding rate, but are scattered (such as fruits and seeds), to foods that are fibrous and result in a low feeding rate, but are abundant (such as bark and buds) (Nakagawa 1989, Nakayama et al. 1999). Our results support this hypothesis. A high degree of bark and bud feeding seems to be a behavioural trait that was acquired by

Japanese macaques when they expanded their range into snowy areas, but this might not be an adaptive trait, since it is known that mass mortality due to malnutrition, and other effects on various population parameters, occur in heavy snow years (Takizawa & Shidaka 1985, Koganezawa & Imaki 1999, Izawa 2009). Japanese macaques migrated into the Japanese archipelago during the mid- to late- Pleistocene (0.78–0.02 Ma), and expanded northward in the post-glacial period (0.01 Ma) following a northward expansion of temperate forests (Wada 1994); they probably had to deal with heavy snow in northern Japan. Therefore, sufficient evolutionary time for them to adapt to snowy conditions behaviourally may not have passed.

The macaques' dietary diversity (in terms of *H'*) was not related to latitude, elevation, or forest type, and was instead associated with snow depth. The opportunistic and generalist nature of macaque feeding is the probable reason for this: bark and buds in snowy habitats are used as alternatives to foliage and other diet categories (such as flowers, fungi, and animal matter) in habitats with little snow (Table 2); thus, an apparent decrease in dietary diversity could be detected.

In the present study, we did not consider the overall effect of body size on diet composition or preference. Japanese macaques in northern and snowy areas are larger than those from southern populations (Hamada & Yamamoto 2010). In general, large-bodied animals are able to absorb more nutrients from foliage than small-bodied ones (Elder 2004). Larger Japanese macaques require more energy and nutrients, and tend to feed predominantly on bark (Watanuki & Nakayama 1993, Nakayama et al. 1999). Large animals tend to cope well in cool climates, due to their relatively low surface area-to-volume ratio. Macaques follow Bergman's rule (Mayr 1970); therefore, latitudinal and environmental gradients in diet can be explained not only by feeding

strategies but also by morphological adaptations to different habitats (Elder 2004).

The effects of the study populations' genetic background on diet preference should also be considered; Imai et al. (2012) found that inter-species variation in the degree of bark feeding may have genetic causes. In addition, quantitative genetic variation is associated with phenotype plasticity in body size of American mink *Neovison vison* in response to the environment (Zalewski & Bartoszewicz 2012).

We did not consider the effect of group size on diet composition. For group-living animals such as primates, within-group competition over foods often affects the diet composition (Whiten et al. 1987) and feeding behaviour (Janson 1985, Tsuji & Takatsuki 2012). In future research, such morphological, genetic, and social traits should be considered, to test more accurate models that explain spatial patterns in the feeding behaviour of macaques, and of other mammals with wider geographical ranges.

In summary, the main determinants of the Japanese macaque's diet were found to be (1) primary productivity, affecting the consumption of fruits and seeds, (2) snow characteristics, affecting the availability of foliage and other food resources, and/or macaque activity, and (3) elevation. Therefore, we wish to emphasise the importance of considering both biotic and abiotic factors on animal feeding ecology. In addition, more emphasis should be placed on snow characteristics. Large-scale reviews of feeding habits, in addition to long-term studies, would contribute to a better understanding of behavioural plasticity and the mechanisms of adaptation to different environments. Our approach also provides insights into both conservation and the testing of behavioural and ecological theories, based on local habitat characteristics.

ACKNOWLEDGEMNTS

We thank K. Izawa, Y. Sugiyama, T. Iwamoto, S. Takeda, T. Kanaizuka, S. Matsuoka, K. Suzuki, K. Kikuma, N. Nakagawa and G. Hanya for providing data. This study was funded by a grant from the AS-HOPE of the Japan Society of Promotion of Science (2010–2011), a Grant-in-Aid from the Department of Academy and Technology of Japan (Nos. 23780160 and 24405018), a Grant for Basic Science Research Projects from the Sumitomo Foundation (2013), and the Corporative Research Fund of Arid Land Research Center, Tottori University (2012–2013).

REFERENCES

Agetsuma N (1995) Dietary selection by Yakushima macaques (*Macaca fuscata yakui*): the influence of food availability and temperature. *International Journal of Primatology* 16: 611-627.

Agetsuma N, Nakagawa N (1998) Effects of habitat differences on feeding behaviors of Japanese monkeys: comparison between Yakushima and Kinkazan. *Primates* 39: 275-289.

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Caski F (eds) *Proceedings of the Second International Symposium on Information Theory,* 267-281. Akadimiai Kiado, Budapest, Hungary.

Anonymous (1994) *A Report on Japanese Macaques in Saitama Prefecture*, Saitama Prefecture, Saitama, Japan.

Anonymous (2012) *R: A Language and Environment for Statistical Computing.* Version 2.15.1. R Foundation for Statistical Computing, Vienna, Austria.

Begon M, Townsend CR, Harper JL (2006) *Ecology: from Individual to Ecosystems.* Blackwell Publishing, Malden, Massachusetts, USA.

Bojarska K, Selva N (2012) Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. *Mammal Review* 42: 120-143.

Burnham, KP, Anderson DR (2002) *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*. Springer-Verlag, New York, USA.

Chijiiwa A (2004) *Movement Patterns and Habitat use of Japanese Macaque (*Macaca fuscata *Blyth, 1875) Troops in a Conifer-Highly Planted Region.* MSc thesis, Doshisha University, Kyoto, Japan.

Clavero M, Prenda J, Deblis M (2003) Trophic diversity of the otter (*Lutra lutra* L.) in temperate and Mediterranean freshwater habitats. *Journal of Biogeography* 30: 761-769.

Díaz-Ruiz F, Delibes-Mateos M, García-Moreno JL, López-Martin JM, Ferreira C, Ferreras P (2013) Biogeographical patterns in the diet of an opportunistic predator: the red fox *Vulpes vulpes* in the Iberian Peninsula. *Mammal Review* 43: 59-70.

Elder AA (2004) Hylobatid diets revisited: the importance of body mass, fruit availability, and interspecific competition. In: Lappan S, Whittaker DJ (eds) *The Gibbons, Developments in Primatology: Progress and Prospects*, 133-159. Springer-Verlag, New York, USA.

Enari H, Sakamaki H (2013) Influence of heavy snow on the feeding behavior of Japanese macaques (*Macaca fuscata*) in northern Japan. *American Journal of Primatology* 75: 534–544.

Enari H, Matsuno H, Maruyama N (2005) Food selection of wild Japanese monkeys (*Macaca fuscata*) utilizing farmland in the northeastern Shirakami Mountains. *Wildlife Conservation Japan* 9: 77-92.

Fujita S, Sugiura H, Mitsunaga F, Shimizu K (2004) Hormone profiles and reproductive

characteristics in wild female Japanese macaques (*Macaca fuscata*). *American Journal of Primatology* 64: 367-375.

Gende SM, Quinn TP (2004) The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. *Canadian Journal of Zoology* 82: 75-85.

Go M (2010) Seasonal changes in food resource distribution and feeding sites selected by Japanese macaques on Koshima Islet, Japan. *Primates* 51: 149-158.

Hamada Y, Yamamoto A (2010) Morphological characteristics, growth, and aging in Japanese macaques. In: Nakagawa N, Nakamichi M, Sugiura H (eds) *The Japanese Macaques*, 27-52. Springer, Tokyo, Japan.

Hanya G (2004) Diet of Japanese macaque troop in the coniferous forest of Yakushima. *International Journal of Primatology* 25: 55-71.

Hanya G, Kiyono M, Yamada A, Suzuki K, Furukawa M, Yoshida Y, Chijiiwa A (2006) Not only annual food abundance but also fallback food quality determines the Japanese macaque density: evidence from seasonal variations in home range size. *Primates* 47: 275-278.

Hanya G, Zamma K, Hayaishi S, Yoshihiro S, Tsuriya Y, Sugaya S, Kanaoka MM, Hayakawa S, Takahata Y (2005) Comparisons of food availability and group density of Japanese macaques in primary, naturally regenerated, and plantation forests. *American Journal of Primatology* 66: 245-262.

Hill DA (1997) Seasonal variation in the feeding behavior and diet of Japanese macaques (*Macaca fuscata yakui*) in lowland forest of Yakushima. *American Journal of Primatology* 43: 305-322.

Hill DA, Agetsuma N (1995) Supra-annual variation in the influence of *Myrica rubra*

fruit on the behavior of a troop of Japanese macaques in Yakushima. *American Journal of Primatology* 35: 241-250.

Hill RA, Dunbar RIM (2002) Climatic determinants of diet and foraging behavior in baboons. *Evolutionary Ecology* 16: 579-593.

Imai H, Suzuki N, Ishimaru Y, Sakurai T, Yin L, Pan W, Abe K, Misaka T, Hirai H (2012) Functional diversity of bitter taste receptor *TAS2R16* in primates. *Biology Letters* 8: 652–656.

Iriante A, Franklin WL, Johnson WE, Redford KH (1990) Biogeographic variation of food habits and body size of the American puma. *Oecologia* 85: 185-190.

Ito TY, Miura N, Lhagvasuren B, Takatsuki S, Tsunekawa A, Jiang Z (2005) Preliminary evidence of a barrier effect of a railroad on the migration of Mongolian gazelles. *Conservation Biology* 19: 945-948.

Ito TY, Miura N, Lhagvasuren B, Enkhbileg D, Takatsuki S, Tsunekawa A, Jiang Z (2006) Satellite tracking of Mongolian gazelles (*Procapra gutturosa*) and habitat shifts in their seasonal ranges. *Journal of Zoology* 269: 291-298.

Iwamoto T (1981) Feeding ecology of gelada and Japanese macaques: on nutritional intake. *Seibutsu-Kagaku* 33: 78-84.

Izawa K (2009) *Research of Wild Japanese Macaques*. Dobutsu-sha, Tokyo, Japan.

Janson C (1985) Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology* 18: 125-138.

Koganezawa M (1975) Food habits of Japanese monkey (*Macaca fuscata*) in the Boso Mountains. In: Kondo S, Kawai M, Ehara A (eds) *Contemporary Primatology*, 380-383. Karger, Basel, Switzerland.

Koganezawa M, Imaki H (1999) The effects of food sources on Japanese monkey home range size and location, and population dynamics. *Primates* 40: 177-185.

Kutner MH, Neter J, Nachtsheim CJ, Li W (2004) *Applied Linear Regression Models*. McGraw–Hill/Irwin, New York, USA.

Lozano J, Moleón M, Virgós E (2006) Biogeographical patterns in the diet of the wildcat, *Felis sylvestris* Schreber, in Eurasia: factors affecting the trophic diversity. *Journal of Biogeography* 33: 1076-1085.

Majolo B, McFarland R, Young C, Qarro M (2013) The effect of climatic factors on the activity budgets of Barbary macaques (*Macaca sylvanus*). *International Journal of Primatology* 34: 500-514.

Mayr E (1970) *Populations, Species, and Evolution*. Belknap Press of Harvard University Press, Cambridge, UK.

Moles AT, Wright IJ, Pitman AJ, Murray BR, Westoby M (2009) Is there a latitudinal gradient in seed production? *Ecography* 32: 78-82.

Nakagawa N (1989) Feeding strategies of Japanese monkeys (*Macaca fuscata*) against deterioration of habitat quality. *Primates* 30: 1-16.

Nakagawa N (1997) Determinants of the dramatic seasonal changes in the intake of energy and protein by Japanese monkeys in a cool temperate forest. *American Journal of Primatology* 41: 267-288.

Nakagawa N, Nakamichi M, Sugiura H (2010) *The Japanese Macaques*. Springer, Tokyo, Japan.

Nakayama Y, Matsuoka S (1999) Food list of Japanese macaques in southwestern Shimokita Peninsula. *Study Report on Japanese Macaques in Shimokita Peninsula* Issue H10: 68-77.

Nakayama Y, Matsuoka S, Watanuki Y (1999) Feeding rates and energy deficits of juvenile and adult Japanese monkeys in cool temperate area with snow coverage. *Ecological Research* 14: 291-301.

Nishimura A (2006) Ecological studies of Japanese macaques living in the northern margin of Kyoto Basin (2): seasonal changes of foraging activities in 2005 and 2006. *The Science and Engineering Review of Doshisha University* 47: 13-20.

O'Donoghue M, Boutin S, Krebs CJ, Zuleta G, Murray DL, Hofer EJ (1998) Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology* 79: 1193–1208.

Owen JG (1990) Patterns of mammalian species richness in relation to temperature, productivity and variance in elevation. *Journal of Mammalogy* 71: 1-13.

Pettorelli N, Vik JO, Mysterud A, Gaillard JM, Tucker CJ, Stenseth NC (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution* 20: 503-510.

Pettorelli N, Ryan S, Muller T, Bunnefeld N, Jędrzejewska B, Lima M, Kausrud K (2011) The normalized difference vegetation index (NDVI): unforeseen successes in animal ecology. *Climate Research* 46: 15-27.

Remonti L, Balestrieri A, Prigioni C (2009) Altitudinal gradient of Eurasian otter (*Lutra lutra*) food niche in Mediterranean habitats. *Canadian Journal of Zoology* 87: 285-291.

Roper TJ, Mickevicius E (1995) Badger *Meles meles* diet: a review of literature from the former Soviet Union. *Mammal Review* 25: 117-129.

Rosenzweig ML (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.

Sawada A, Sato H, Inoue E, Otani Y, Hanya G (2014) Mycophagy among Japanese

macaques in Yakushima: fungal species diversity and behavioral patterns. *Primates* 55: 249-257.

Schoener TW (1971) Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2: 369-404.

Stephens DW, Krebs JR (1986) *Foraging Theory.* Princeton University Press, Princeton, USA.

Sugiyama Y, Ohsawa H (1982) Population dynamics of Japanese monkeys with special reference to the effect of artificial feeding. *Folia Primatologica* 39: 238-263.

Suzuki A (1965) An ecological study of wild Japanese monkeys in snowy areas - focused on their food habits. *Primates* 6: 31-72.

Takagi M, Nishimura A, Mitsuta S (2002) An ecological study of Japanese macaques at Ujitawara-cho, Kyoto Prefecture (2): ranging and feeding patterns. *The Science and Engineering Review of Doshisha University* 42: 221-235.

Takasaki H (1981) Troop size, habitat quality, and home range area in Japanese macaques. *Behavioral Ecology and Sociobiology* 9: 277-281.

Takeda S, Kanazawa T, Shimizu S (1983) Vegetation and food habits of Japanese macaques inhabiting Minoo (A troop) in fall. *Report on Japanese Macaques in Minoo Mountain* Issue S57: 35-56.

Takeda S, Kanazawa T, Shimizu S (1984) Vegetation and food habits of Japanese macaques inhabiting Minoo (A troop) in spring. *Report on Japanese Macaques in Minoo Mountain* Issue S58: 46-63.

Takeda S, Kanazawa T, Shimizu S (1985a) Vegetation and food habits of Japanese macaques inhabiting Minoo (A troop) in summer. *Report on Japanese Macaques in Minoo Mountain* Issue S59: 31-42.

Takeda S, Kanazawa T, Shimizu S (1985b) Vegetation and food habits of Japanese macaques inhabiting Minoo (A troop) in winter. *Report on Japanese Macaques in Minoo Mountain* Issue S59: 43-52.

Takizawa H, Shidaka K (1985) On the large scale disappearance of the monkeys from Kamuri-A and C troop of wild Japanese monkey (*Macaca fuscata fuscata*) troops in Mt. Hakusan. *Research Report of Hakusan Nature Conservation Center, Ishikawa Prefecture* 16: 49-63.

Ting S, Hartley S, Burns KC (2008) Global patterns in fruiting seasons. *Global Ecology and Biogeography* 17: 648-657.

Tsuji Y (2010) Regional, temporal, and Interindividual variation in the feeding ecology of Japanese macaques. In: Nakagawa N, Nakamichi M, Sugiura H (eds) *The Japanese Macaques*, 99-127. Springer, Tokyo, Japan.

Tsuji Y, Fujita S, Sugiura H, Saito C, Takatsuki S (2006) Long-term variation in fruiting and the food habits of wild Japanese macaques on Kinkazan Island, northern Japan. *American Journal of Primatology* 68: 1068-1080.

Tsuji Y, Hanya G, Grueter CC (2013) Feeding strategies of primates in temperate and alpine forests: comparison of Asian macaques and colobines. *Primates* 54: 201–215.

Tsuji Y, Takatsuki S (2012) Interannual variation in nut abundance is related to agonistic interactions of foraging female Japanese macaques (*Macaca fuscata*). *International Journal of Primatology* 33: 484-512.

Tsuji Y, Wada K, Watanabe K (2011) Woody plants eaten by wild Japanese macaques. *Primate Research* 27: 27-49.

Tsuji Y, Wada K, Watanabe K (2012) Non-woody plant diet of wild Japanese macaques: herbaceous plants, ferns, fungi, seaweeds and animal matter. *Primate Research* 28:

21-48.

Uehara S (1977) A biogeographic study of adaptation of Japanese monkeys (*Macaca fuscata*), from view point of food habits – an essay on reconstruction of the history of Japanese monkeys' distribution. In: Kato Y, Nakao S, Umesao T (eds) *Morphology, Evolution and Primates*, 189-232. Chuokoron-Sha, Tokyo, Japan.

Villafuerte R, Vinuela J, Blanco JC (1998) Extensive predator persecution caused by population crash in a game species: the case of the red kite and rabbits in Spain. *Biological Conservation* 84: 181-188.

Virgós E, Llorente M, Cortés Y (1999) Geographical variation in genet (*Genetta genetta* L.) diet: a literature review. *Mammal Review* 29: 119-128.

Virgós E, Mangas JG, Blanco-Aguiar JA, Garrote G, Almagro N, Viso RP (2004) Food habits of European badgers (*Meles meles*) along an altitudinal gradient of Mediterranean environments: a field test of the earthworm specialization hypothesis. *Canadian Journal of Zoology* 82: 41-51.

Wada K (1964) Some observations on the life of monkeys in a snowy district of Japan. *Physiology and Ecology* 12: 151-174.

Wada K (1994) *How Japanese Macaques Overwinter*. Nobunkyo, Tokyo, Japan.

Watanuki Y, Nakayama Y (1993) Age difference in activity pattern of Japanese monkeys: effects of temperature, snow, and diet. *Primates* 34: 419-430.

Whiten A, Byrne RW, Henzi SP (1987) The behavioral ecology of mountain baboons. *International Journal of Primatology* 8: 367-388.

Zalewski A (2004) Geographical and seasonal variation in food habits and prey size of the European marten *Martes martes*. In: Harrison DJ, Fuller AK, Proulx G (eds) *Martens and Fishers (*Martes*) in Human-Altered Environments: an International*

Perspective, 77-98. Academic Publishers, Dordrecht, Netherlands.

Zalewski A, Bartoszewicz M (2012) Phenotypic variation of an alien species in a new environment: the body size and diet of American mink over time and at local and continental scales. *Biological Journal of the Linnean Society* 105: 681-693.

Zhou YB, Newman C, Xu WT, Buesching CD, Zalewski A, Kaneko Y, Macdonald DW, Xie ZQ (2011) Biogeographical variation in the diet of Holarctic martens (genus *Martes*, Mammalia: Carnivora: Mustelidae): adaptive foraging in generalists. *Journal of Biogeography* 38: 137-147.

Table 1 Locations of the study sites in the studies of Japanese macaques included in this review, with diet composition and trophic diversity (Shannon-Wiener index, *H′*) based on food lists.

No.[a]	Study sites	Climate	Geographical variables		Environmental variables					Diet composition (%)[b]							*H′*	Reference
			Latitude (º)	Elevation (m)	Mean temperature (ºC)	Annual rainfall (mm)	Snow depth (cm)	Snow duration (# months)	NDVI	Foliage	Flowers	Fruits & Seeds	Bark & Buds	Fungi	Animal matter	Others		
1	Shimokita	Deciduous	41.15	480	9.8	1295.6	114.2	6	6958	21.4	7.9	18.4	29.5	2.7	5.2	14.8	0.75	Tsuji et al. (2011, 2012), Nakayama & Matsuoka (1999)
2	Shirakami	Deciduous	40.52	350	10.2	1183.1	149.8	6	5028	16.7	2.8	25.0	22.8	0.0	0.0	2.8	0.51	Tsuji et al. (2011, 2012), Enari et al. (2005)
3	Okunikkawa	Deciduous	38.33	650	10.0	1532.5	73.3	6	6004	21.6	4.3	21.6	42.2	6.9	1.7	1.7	0.65	Tsuji et al. (2011, 2012)
4	Kinkazan	Decid	38.29	230	11.6	1067.	4.4	6	4833	21.	6.8	17.	6.	2.	1	9.	6.0	0.7	Tsuji et al. (2006,

		uo us				1				9		9	2	1			9	2011, 2012), Agetsuma and Nakagawa (1998)
5	Iitate	De cid uo us	37. 68	65 0	10.0	13 25. 1	36. 8	6	59 58	2 2. 2	6. 7	3 7. 8	2 2. 2	4. 4	4. 4	2. 2	0. 6 9	Tsuji et al. (2011, 2012)
6	Mt. Azuma	De cid uo us	37. 74	10 50	7.5	17 93. 9	14 2.8	6	46 43	3 9. 2	0. 0	2 1. 6	3 5. 3	3. 9	0. 0	0. 0	0. 5 2	Tsuji et al. (2011, 2012)
7	Kurobe	De cid uo us	36. 80	15 50	11.6	29 64. 7	10 3.2	7	45 53	3 5. 7	7. 1	1 6. 7	3 1. 0	0. 0	0. 0	9. 5	0. 6 3	Tsuji et al. (2011, 2012)
8	Nikko	De cid uo us	36. 75	95 0	6.9	21 69. 0	85. 0	7	50 91	3 1. 8	3. 7	2 0. 6	3 9. 7	1. 4	0. 9	1. 9	0. 5 9	Tsuji et al. (2011, 2012)
9	Shiga Heights	De cid uo us	36. 73	95 0	10.5	18 81. 5	23 3.4	7	58 58	1 4. 4	6. 4	1 6. 0	4 1. 7	3. 0	3. 2	1 5. 2	0. 7 0	Tsuji et al. (2011, 2012), Suzuki (1965)
1 0	Kamikouchi	De cid uo us	36. 58	23 40	9.4	13 97. 3	10 3.2	7	53 26	3 4. 2	0. 0	2 0. 8	3 3. 3	3. 5	7. 4	0. 9	0. 6 1	Tsuji et al. (2011, 2012), Suzuki (1965)
1 1	Hakusan	De cid uo us	36. 26	10 00	12.7	27 93. 9	11 7.6	6	46 27	1 3. 5	5. 2	1 7. 9	3 6. 7	0. 4	4. 8	2 1. 4	0. 7 0	Tsuji et al. (2011, 2012), Suzuki

																		(1965)
12	Chichibu	Deciduous	35.93	80	13.1	13 33.1	13.0	5	71 44.0	1	3.5	3 5.1	2 9.8	1.8	7.0	8.8	0.69	Tsuji et al. (2011, 2012), Anonymous (1994)
13	Okutama	Deciduous	35.81	42 0	11.9	16 08.5	13.0	5	71 60	2 3.2	8.6	3 0.5	2 8.2	0.0	0.9	8.6	0.66	Tsuji et al. (2011, 2012)
14	Tanzawa	Evergreen	35.50	74 0	15.8	21 88.8	2.4	3	72 55	1 6.7	0.0	3 0.0	1 6.7	0.0	0.0	3 6.7	0.58	Tsuji et al. (2011, 2012)
15	Boso	Evergreen	35.12	32 0	13.8	20 12.1	0.0	0	53 16	2 7.8	3.0	1 9.3	1 9.3	0.3	2.7	2 7.6	0.68	Tsuji et al. (2011, 2012), Koganezawa (1975)
16	Kyoto Basin	Evergreen	35.08	42 0	15.9	14 91.3	3.8	4	61 43	4 4.1	7.4	2 2.1	1 4.7	0.0	0.0	1 1.8	0.62	Tsuji et al. (2011, 2012), Nishimura (2006)
17	Tsuchiyama	Evergreen	34.97	73 0	13.0	16 03.0	20.8	4	69 60	4 2.1	1 2.3	2 2.8	1 7.5	0.9	1.8	2.6	0.64	Tsuji et al. (2011, 2012), Chijiiwa (2004)
18	Nukata	Evergreen	34.91	16 0	15.5	20 21.9	3.2	3	79 00	2 2.8	8.9	3 7.3	2 7.2	0.6	0.6	2.5	0.62	Tsuji et al. (2011, 2012)
19	Uji	Evergreen	34.86	20 0	15.9	14 91.3	3.8	4	70 18	1 9.0	5.2	2 0.7	1 9.0	3.4	3.4	2 9.3	0.74	Tsuji et al. (2011, 2012),

		n																	Takagi et al. (2002)
20	Minoo	Evergreen	34.85	350	16.0	1282.7	0.4	2	65	28.8	10.3	2.9	2	1.5	0.3	3	1	3.1	0.72	Tsuji et al. (2011, 2012), Takeda et al. (1983, 1984, 1985a, 1985b)
21	Mt. Hiei	Evergreen	35.05	850	15.9	1491.3	3.8	4	66	20.2	5.3	9.2	8.6	7	7	2.3	4	0.74	Tsuji et al. (2011, 2012)
22	Arashiyama	Evergreen	35.01	155	15.9	1491.3	3.8	4	60	21.9	8.3	8.3	2.8	1	0.3	0	8.5	4	0.60	Tsuji et al. (2011, 2012)
23	Gagyuzan	Evergreen	34.83	480	14.2	1204.2	0.8	3	66	42.9	8	4.1	1.0	1	1.2	0	0	0.57	Tsuji et al. (2011, 2012)
24	Miyajima	Evergreen	34.28	430	12.6	1949.6	2.6	4	71	19.99	5	0.8	6.7	2	1.3	1	9.9	2.9	0.73	Tsuji et al. (2011, 2012)
25	Mt. Kawaradake	Evergreen	33.69	500	15.7	1767.1	0.0	0	68	29	4.7	2	9.8	3	0	2	5.8	2	0.60	Tsuji et al. (2011, 2012)
26	Takasakiyama	Evergreen	33.25	320	16.4	1644.7	0.2	1	61	54	6.9	4	0.7	2	4.1	0.6	5	7.8	0.72	Tsuji et al. (2011, 2012)
27	Koshima	Evergreen	31.45	600	18.2	2598.	0.0	0	42	49	2.2	1	3.3	1	4	1.6	5	6.2	0.76	Tsuji et al. (2011,

		ree n				7				8		8	9			5	4	2012), Iwamoto (1981), Go (2010)
28	Yakushima (coastal)	Evergreen	30.37	200	19.4	44 77.2	0.0	0	75 99	2 8.7	6.2	3 3.6	1 3.3	0.6	5.9	1 1.7	0.7 0	Tsuji et al. (2011, 2012), Agetsuma (1995), Agetsuma & Nakagawa (1998), Hill (1997), Sawada et al. (2014)
29	Yakushima (coniferous)	Evergreen	30.34	1100	12.4	49 86.0	0.0	0	74 29	2 7.8	7.8	2 6.7	3.3	6.7	1 7.8	1 0.0	0.7 5	Tsuji et al. (2011, 2012), Hanya (2004)
	Deciduous forest (n = 13)		37.58	87 8	10.4	17 18.9	91.5	6.2	56 30	2 3.8	4.9	2 3.1	3 4.5	3.1	3.4	7.2	0.6 5	
	Evergreen forest (n = 16)		33.97	43 8	15.4	21 06.3	2.8	2.3	66 26	2 7.3	7.2	2 5.1	1 7.1	1.1	4.6	1 7.5	0.6 7	
	U values		208.0***	161.5	5.0** *	79.0^{NS}	205.0***	208.0***	47.0*	7 7.0^{NS}	6 3.5^{NS}	7 6.5^{NS}	2 0.0**	1 4 3.0^{NS}	1 0 2.5^{NS}	5 1.5*		90.5^{NS}
	Grand mean (n = 29)		35.59	63 6	13.2	19 32.6	42.6	4.0	61 80	2 5.7	6.2	2 4.2	2 4.9	2.0	4.1	1 2.9	0.6 6	

[a]See Fig. 1 for each location. [b]See Tsuji *et al*. (2011, 2012). ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, NS: not significant. NDVI: normalized difference vegetation index. H': Shannon-Wiener index.

Table 2 Results from generalized linear models used to predict diet composition (foliage, fruits and seeds, and bark and buds) and dietary diversity (*H'*) of Japanese macaques.

Variables	Diet composition							*H'*	
	Foliage		Fruits & Seeds			Bark & Buds			
	1)	2)	1)	2)	3)	1)	2)	1)	2)
Intercept	25.577 ± 1.575 (*t* = 16.46, *P* < 0.001)	25.577 ± 1.576 (*t* = 16.38, *P* < 0.001)	4.215 ± 1.219 (*t* = 19.38, *P* < 0.001)	4.215 ± 1.219 (*t* = 19.40, *P* < 0.001)	4.215 ± 1.219 (*t* = 19.40, *P* < 0.001)	4.295 ± 1.219 (*t* = 20.02, *P* < 0.001)	4.296 ± 1.219 (*t* = 19.82, *P* < 0.001)	0.600 ± 0.011 (*t* = 50.51, *P* < 0.001)	0.600 ± 0.011 (*t* = 50.28, *P* < 0.001)
Latitude	—	—	—	—	—	—	1.793 ± 2.739 (*t* = 0.75, *P* = 0.462)	—	—
Elevation	**3.281 ± 1.820 (*t* = 1.79, *P* = 0.086)**	3.181 ± 1.831 (*t* = 1.73, *P* = 0.096)	—	—	—	-2.284 ± 1.524 (*t* = -1.50, *P* = 0.146)	-1.663 ± 1.716 (*t* = -0.97, *P* = 0.342)	—	—
Mean temperature	—	—	—	—	-1.119 ± 1.9	—	—	—	—

					9 5 4 (*t* = -0.99, *P* = 0.330)			
Annual rainfall	—	—	—	—	—	—	—	0 ± 0 . 0 1 (*t* = 0.87, *P* = 0.393)
Snow depth	- ± 1 2 . . 8 7 0 0 (*t* = -1.50, *P* = 0.146)	**- ± 1 . 3 . 9 4 9 1** (*t* = -1.71, *P* = 0.099)	—	—	—	5 ± 1 . . 7 7 7 8 (*t* = 3.24, *P* = 0.003)	**5 ± 1 . . 3 8 7 7** (*t* = 2.86, *P* = 0.009)	**- ± 0 . 0 . 0 1 2** (*t* = -1.53, *P* = 0.137)	**- ± 0 . 0 . 0 1 2** (*t* = -1.45, *P* = 0.159)
Snow duration	—	—	—	- ± 1 1 . 3 . 4 4 0 (*t* = -1.04, *P* = 306)	- ± 1 2 . 9 7 3 8 (*t* = -1.44, *P* = 0.162)	**5 ± 1 . . 8 7 4 8** (*t* = 3.28, *P* = 0.003)	4 ± 2 . . 3 6 9 4 (*t* = 1.662, *P* = 0.110)	—	—
NDVI	—	- ± 1 1 . . 7 5 9 4 (*t* = -0.86, *P* = 0.399)	**3 ± 1 . . 6 2 4 5** (*t* = 2.92, *P* = 0.007)	**3 ± 1 . . 1 3 3 4** (*t* = 2.34, *P* = 0.027)	**3 ± 1 . . 4 3 0 7** (*t* = 2.49, *P* = 0.020)	—	—	—	—
AIC	210.75	211.91	19	19	19	19	19	-6	-6

			6	7	8	8	9	7	6
			.	.	.	.	.	.	.
			7	5	4	4	7	4	2
			5	6	4	3	7	0	3
ΔAIC	—	1	—	0	1	—	1	—	1
		.		.	.		.		.
		1		8	6		3		1
		6		1	9		4		7

NDVI: normalized difference vegetation index. AIC: Akaike's information criteria. Models with difference of AIC (ΔAIC) was less than 2.0 were treated as identical. *H'*: Shannon-Wiener index.

Note that coefficients wereestimated after all explanatory variables had been standardized.

Figure legends

Figure 1 Locations within Japan of the 29 reviewed studies on the diet of Japanese macaques *Macaca fuscata*. Filled circles represent study sites located in deciduous forests (shown as the grey area), and open circles represent study sites located in evergreen forests (shown as the white area; Tsuji 2010). 1, Shimokita Peninsula; 2, Shirakami; 3, Okunikkawa; 4, Kinkazan; 5, Iitate; 6, Mt. Azuma; 7, Kurobe; 8, Nikko; 9, Shiga Heights; 10, Kamikouchi; 11, Hakusan; 12, Chichibu; 13, Okutama; 14, Tanzawa; 15, Boso Peninsula; 16, Kyoto Basin; 17, Tsuchiyama; 18, Nukata; 19, Uji; 20, Minoo; 22, Mt. Hiei; 23, Arashiyama; 24, Miyajima; 25, Kawaradake; 26, Takasakiyama; 27, Koshima; 28, Yakushima (coastal forest); 29, Yakushima (coniferous forest; see also Table 1).

Figure 2 Relationships between geographical and environmental variables and diet composition: a) elevation and %foliage, b) snow depth and %foliage, c) NDVI and %fruits and seeds, d) snow depth and %bark and buds, and e) snow duration and %bark and buds. Each filled circle represents a study site.

Figure 3 Relationships between snow depth and dietary diversity (in terms of *H'*). Each filled circle represents a study site.

Fig. 1

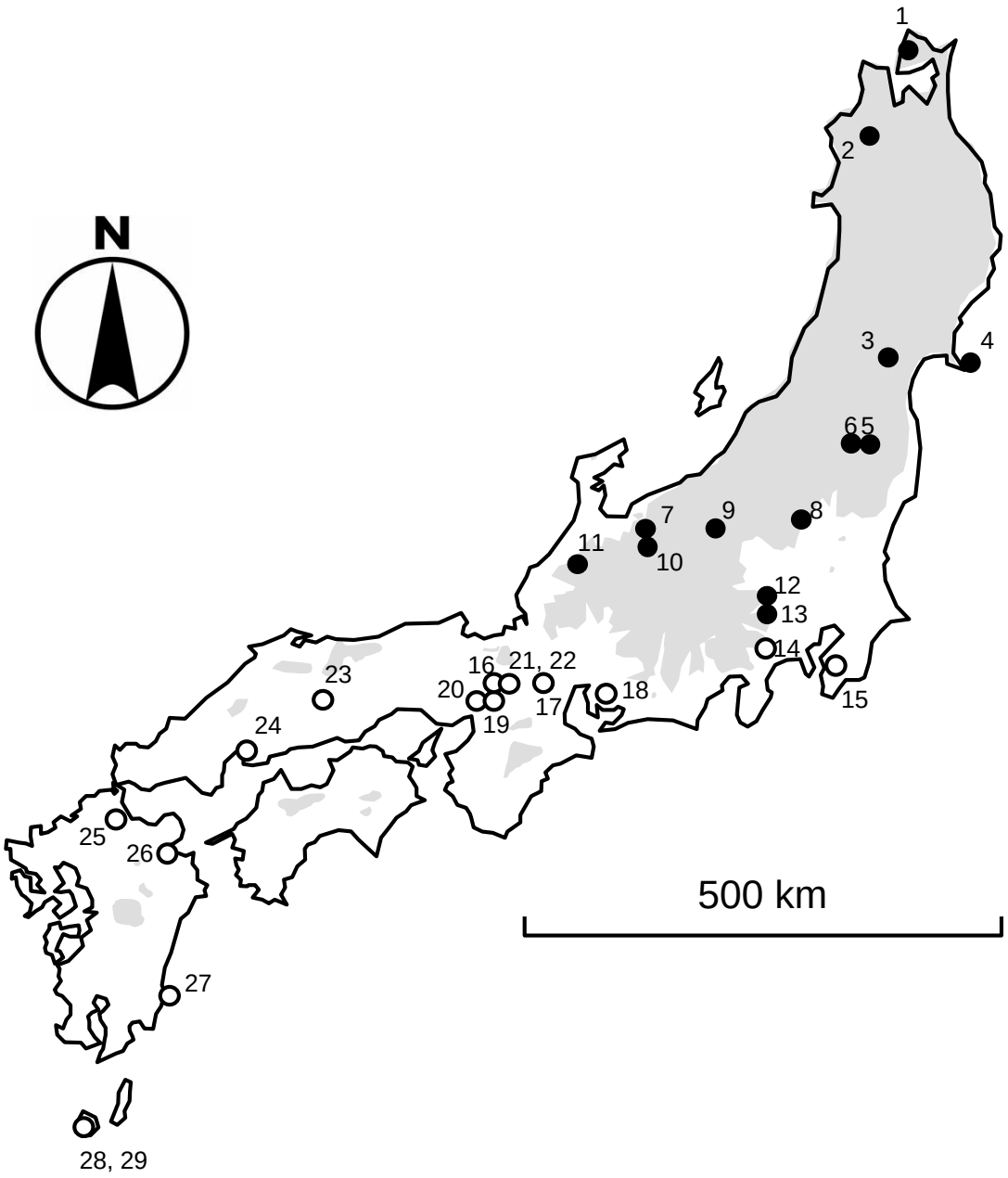

Fig. 2

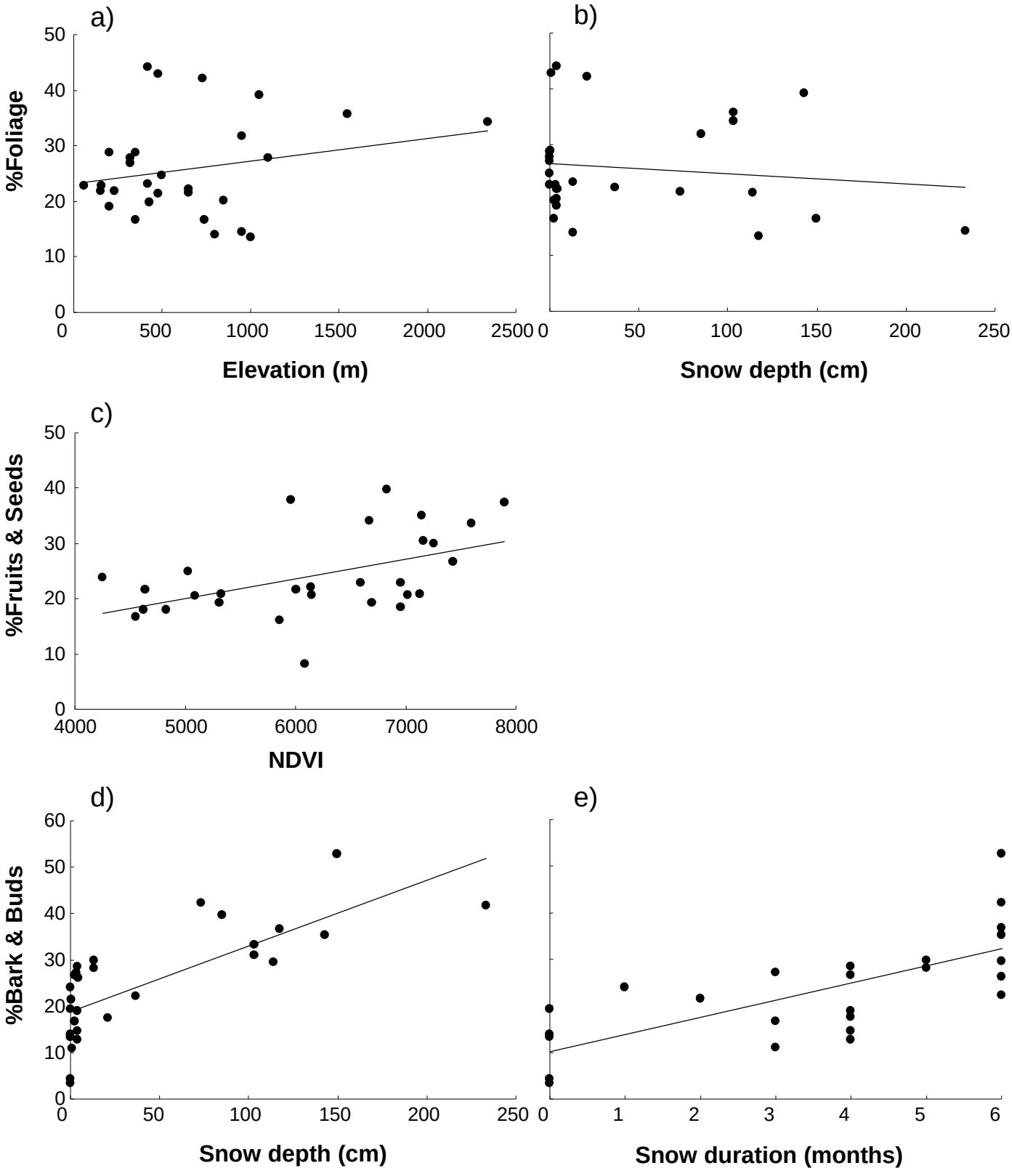

Fig. 3